2005. The Journal of Arachnology 33:7–15

SCYTODES VS. *SCHIZOCOSA*: PREDATORY TECHNIQUES AND THEIR MORPHOLOGICAL CORRELATES

Robert B. Suter: Department of Biology, Vassar College, 124 Raymond Avenue, Poughkeepsie, New York 12604 USA. E-mail: suter@vassar.edu

Gail E. Stratton: Department of Biology, University of Mississippi, University, Mississippi 38677 USA. E-mail: byges@olemiss.edu

ABSTRACT. Wolf spiders (Lycosidae) typically subdue prey using their legs for capture and their fangs for the injection of venom. Spitting spiders (Scytodidae), in contrast, subdue prey by entangling them, at a distance, in a spitted mixture of silk, glue, and venom that immobilizes and may also kill them. We selected individuals of *Schizocosa duplex* (Lycosidae) and *Scytodes* sp. (Scytodidae) of approximately the same mass and carapace width to provide a quantitative assessment of their relative allocations of biomass to morphological features that might be expected to vary with prey-capture technique. As expected, the wolf spiders allocated significantly more to legs, chelicerae, and fangs, and significantly less to the venom glands, than did the spitting spiders. Further comparisons of the legs and chelicerae of the two species provided surprises. First, the legs of *Scytodes* were 42% longer than those of *Schizocosa* despite smaller overall allocation to the legs in *Scytodes*. And second, although the relative sizes of the chelicerae differ greatly, the shapes of the chelicerae of *Schizocosa* and *Scytodes* were not significantly different despite the radically different tasks those structures must fulfill.

Keywords: Spitting spider, wolf spider, resource allocation, allometry

Spitting spiders (Araneae, Scytodidae) are renowned for their eponymous method of subduing prey and, at least occasionally, deterring predators (Gilbert & Rayor 1985; Jackson & Pollard 2001). They eject a glutinous mixture of silk, adhesive, and toxin, all from their enlarged venom glands (Monterosso 1928; Millot 1929, 1930; Bristowe 1931; Dabelow 1958; MacAlister 1960; Kovoor 1987; Foelix 1996), that rapidly immobilizes the insects and spiders that typically constitute their diet (Nentwig 1985).

What distinguishes this peculiar way of subduing prey from other methods used by spiders is not the use of glue-adorned fibers. Such a combination of materials typifies the prey capture spirals of araneid orb-weavers (e.g., Peters 1987; Foelix 1996; Opell 1997) and the webs of other spiders that produce sticky silk from their opisthosomal spinnerets. Rather, the uniqueness of the method is attributable both to the prosomal source of the materials, the venom glands (Kovoor 1987; Kovoor & Zylberberg 1972), and to the forceful and directed ejection of the mixture (Millot 1930; Bristowe 1931).

Our interest in spitting spiders began with a quest to quantify their expectorant capabilities, but quickly turned to the suite of morphological characteristics that, together, appear to contribute to the overall effectiveness of spitting as a predatory method. These characteristics include (a) venom glands large enough to secrete and store quantities of silk, glue and venom sufficient for multiple predation attempts, (b) ducts and nozzles large enough to accommodate rapid flows of glutinous material and (c) sensory structures capable of conveying adequately accurate targeting information. We know from earlier work that scytodid spiders have disproportionately large venom glands (e.g. Millot 1929), that the secretory epithelia of these glands extend into the chelicerae (Kovoor & Zylberberg 1972), and that the orifice through which the spit is ejected is located near the base of the fang (Kovoor & Zylberberg 1972) rather than at its usual location near the fang's distal end (Foelix 1996). We also know that these spiders are primarily nocturnal hunters that appear to use their legs in sensory exploration of their environment, detecting prey via either vibrations or viadirect tactile sensations (Nentwig 1985). The structure and orientations of their eyes, then, may be of little

consequence for the triggering and the accuracy of their spitting, but the structure of the legs may be crucial.

To assess quantitatively the morphological correlates of the predatory specialization seen in spitting spiders, we compared *Scytodes thoracica* (Latreille 1802) and *S. fusca* Walckenaer 1837 with a comparable sized wolf spider, *Schizocosa duplex* Chamberlin 1925 (Araneae, Lycosidae). Like scytodids, the wolf spiders are often nocturnal hunters that generally do not use webs in prey capture. Unlike the spitting spiders, however, the wolf spiders lunge and grab prey with their legs and bite the prey immediately. We knew at the outset that these differences in predatory technique are strongly reflected in the directly supporting morphology–the wolf spider's legs, chelicerae, and fangs are more robust than those of the spitting spider, and the spitting spider's venom glands are substantially larger than those of the wolf spider (Monterosso 1928; Millot 1929, 1930; Foelix 1996)–although those specific comparisons have not previously been made in the literature.

These differences, we assumed, also reflect a history of selective pressures that have modified the allocation of resources (Huxley 1932; Calder 1984) within developing spiders. For example, physiological and metabolic resources that could have been devoted to the production of eggs in an adult female wolf spider are, instead, devoted to the production and maintenance of stout legs and chelicerae. Our adaptionist assumption was that the differences we would detect between these two kinds of spiders mark differences in natural selection that moved each lineage toward an optimal allocation of physiological resources. At the same time, we recognized that the very disparate lineages of the lycosids and the scytodids could contribute substantively to the differences we would detect. For example, the upright, cursorial habit of wolf spiders differs fundamently from the usually supine, sedentary habit of spitting spiders, and the consequent disparity in morphology need not be directly related to differences in predatory techniques.

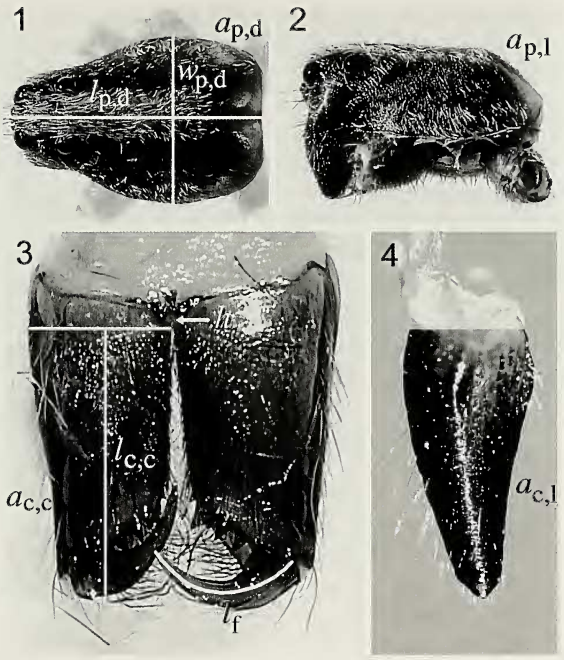
METHODS

Spiders.—We used 12 adults (8 females, and 4 males) of the wolf spider, *Schizocosa duplex*, drawn from the collection of P. Miller and G. Stratton, maintained in 80% alcohol, at the Department of Biology, University of Mississippi. All were originally collected in Mississippi (MS., Panola County, nr Sardis Dam, Sandstone Nature Trail 34° 23.616 N, 89° 47.496 W., 5 May 2002). Our specimens of the spitting spiders were provided, live, by James Carrel and Hank Guarisco (9 adult female *S. thoracica*) from Florida (Fl., Highlands County, 10 km S. of Lake Placid, Archbold Biological Station; FL, Santa Rosa County, Pensacola), and by Gerald Baker (1 adult female *S. fusca*) from Mississippi (MS., Oktibbeha County, in Starkville). Subsequent to their use in biomechanics studies, the spitting spiders were preserved in 80% alcohol until we used them in this study. We have deposited voucher specimens in the Mississippi Entomological Museum.

Our use of both sexes in the wolf spider species *S. duplex* and of two species in the spitting spider genus *Scytodes* could, in theory, have complicated our analyses and skewed our results. Most spider species are sexually dimorphic, and this is the case even among the Lycosidae (Walker & Rypstra 2001, 2002) in which the dimorphism is less striking than in many other families of spiders (Foelix 1996). Similarly, species within the same genus can differ both in overall size and in the relative sizes of individual parts. These differences notwithstanding, we pooled the two wolf spider sexes and pooled the two spitting spider species, electing to increase our sample size despite the small expected increase in variance that might result from the pooling.

Morphometry.—Spiders preserved in alcohol lose mass due to evaporation when exposed to air. To minimize the consequent inaccuracies, we weighed the spiders and their parts, to the nearest 0.1 mg, during < 2 min exposure to air after initially removing surface moisture by blotting with dry filter paper. Because very small objects, such as the chelicerae and venom glands, are especially susceptible to rapid drying and thus to spurious mass measurements, we also made digital images of the structures in which we were interested.

In one series of images, we devoted a single frame (6.1 MP, Nikon D100) to an entire but dismembered spider. These images showed dorsal views of the separated prosoma and opisthosoma and lateral views of the legs and



Figures 1–4.—Image-derived morphometry methods illustrated for *Schizocosa duplex*. Lengths, widths, and areas are represented by their italic initials. The first subscript represents the structure (e.g., prosoma, chelicera, fang) and the second subscript designates the view (e.g., dorsal, lateral, caudal). The position of the horizontal line (3), which delimited one end of $l_{c,c}$, was determined by the location of the bottom margin of the hinge (h) around which the jaws rotate. Volumes were calculated as described in the text.

pedipalps. In another series of images collected via dissecting microscope (Olympus SZX12) and dedicated digital camera (Olympus 750), we devoted a single frame (0.32 MP) each to dorsal, lateral and frontal views of the prosoma (including chelicerae), caudal and lateral views of the chelicerae (after detachment from the prosoma), and dorsal and lateral views of the venom glands. We measured lengths, widths, and areas of the structures in these images using NIH Image (NIH shareware) and MetaMorph (Universal Imaging Corporation).

We used a scanning electron microscope (Amray 1200C) to visualize details on the anterior surface of two spiders that had been freeze-dried and sputter coated with gold and palladium (80:20).

The image-based measurements allowed us to estimate the volume of each prosoma, chelicera, venom gland and leg. For example, we estimated the volume of the prosoma of a *Schizocosa duplex* (Figs. 1 & 2) as the product of the area of the prosoma's dorsal view ($a_{p,d}$) and the average height of the prosoma, calculated as the area of the prosoma's lateral view ($a_{p,l}$) divided by the length of the prosoma ($l_{p,d}$). Thus the estimated volume of the prosoma (v_p) is

$$v_p = a_{p,d} \cdot (a_{p,l}/l_{p,d}).$$

If the prosoma were rectangular in three planes, this measure of v_p would accurately reflect the structure's true volume. The fact that the prosoma is not rectangular means that v_p overestimates its true volume.

We applied the same method in estimating the volumes of the prosoma and chelicerae of all of the spiders and the venom glands of the spitting spiders (Figs. 1–4). To estimate the volume of the legs of all of the spiders and the venom glands of the wolf spiders, we assumed these structures to be approximately cylindrical. Thus we estimated the volume of a leg (v_l), for example, by taking its area (a_l) divided by its length (l_l) as double its average radius (r_l), and then calculating volume as

$$v_l = l_l \cdot \pi\, r_l^2.$$

One of the wolf spiders in the study was

missing one of its chelicerae and four of the spitting spiders were missing a single leg each. In each of these cases we assumed that the missing structure had the same dimensions as its contralateral mate. Although we measured opisthosomal volumes and masses, we have ignored these measurements in the present study. This is because, as the part of the body that is most extensible (Foelix 1996), it is most subject to the volume and mass fluctuations that accompany changes in feeding history and reproductive state and thus is less likely to provide reliable comparative data.

RESULTS

Morphometry.—The representatives of the two families of spiders were not significantly different in size as measured by the width of the carapace (*Scytodes*: 2.78 ± 0.17 mm, mean ± SE; *Schizocosa*: 2.43 ± 0.057 mm; $t = 2.06$, $P = 0.053$), the mass of the body not including the opisthosoma (*Scytodes*: 17.5 ± 1.93 mg; *Schizocosa*: 19.2 ± 1.26 mg; $t = -0.77$, $P = 0.448$), and the volume of the body not including the opisthosoma (*Scytodes*: 22.26 ± 2.76 mm^3; *Schizocosa*: 21.63 ± 1.02 mm^3; $t = -0.23$, $P = 0.822$). These data confirmed our initial assumption that the two groups of spiders were grossly similar in size.

For some structures (e.g., the legs and the prosoma), we had measures of both mass and volume. Not surprisingly, these measures were closely correlated but not identical, with higher correlations in the spitting spiders than in the wolf spiders (Fig. 5). These highly significant correlations suggest that the use of volume measurements as proxies for mass measurements is justified. As noted above, this substitution is also necessitated by the difficulties encountered in accurately weighing very small structures such as the chelicerae of the spitting spiders and the venom glands of the wolf spiders.

Despite the similarity in the overall sizes of the spitting and wolf spiders, we found striking differences in the sizes of their component parts (Table 1). The average spitting spider had a 36% larger prosoma and had venom glands that were 32 times as voluminous than those of the average wolf spider. The venom glands of *Scytodes* were also, as noted in the literature, conspicuously more complex in shape than those of *Schizocosa* (Fig. 6). At the same time, the legs and chelicerae of *Scytodes* were 42% and 83% smaller, as measured by volume, than those of *Schizocosa*, respectively. The linear dimensions of the legs and chelicerae, of interest in part because they have implications for biomechanical strength, also revealed major differences (Table 1). The legs of the spitting spiders were 42% longer, but 38% less wide in the dorso-ventral direction, than those of the wolf spiders. The chelicerae of *Scytodes* had about the same ratio of length to width (1.84: 1) as the chelicerae of *Schizocosa* (1.79: 1), but were 46% shorter and 41% narrower. Finally, the fangs of the spitting spiders were only 21% as long as the fangs of the wolf spiders (compare Figs. 3 & 8, showing *Schizocosa*, with Figs. 10 & 11, showing *Scytodes*).

Resource allocation.—Several of the conspicuous differences in the allocation of resources by these spiders are readily visible (Figs. 7–11). A wolf spider's chelicerae, for example, are proportionately much more massive relative to the rest of its "face" than are the chelicerae of the spitting spider. In fact, the legs and jaws, together, in the spitting spiders comprise only 22% of the total volume of the measured structures while in the wolf spider they comprise 44% (Fig. 12). In contrast, and as expected from the data in Table 1, the venom glands in *Schizocosa* comprise only 0.3% of the total (0.6% of prosomal volume) while in *Scytodes* they comprise nearly 10% (15% of prosomal volume).

Another component of the resource allocation differences can be seen in a comparison of the anterior four legs to the posterior four legs (Table 1). With respect to leg lengths, the spitting spiders have, on average, 37% longer forelegs than hind legs while the wolf spiders' forelegs are 25% shorter than the hind legs. With respect to leg widths, these relationships are reversed: the spitting spiders' forelegs are 9% narrower than their hind legs while the wolf spiders have forelegs that are, on average, 15% broader (in the dorsal-ventral direction) than the hind legs.

DISCUSSION

When capturing prey, the wolf spider, *Schizocosa*, grabs and bites, often using all eight legs in the grab and enveloping the prey in a leggy basket, or it may hang on to a prey item and hold it at a safe distance using the scopular hairs found on the tarsi and metatarsi,

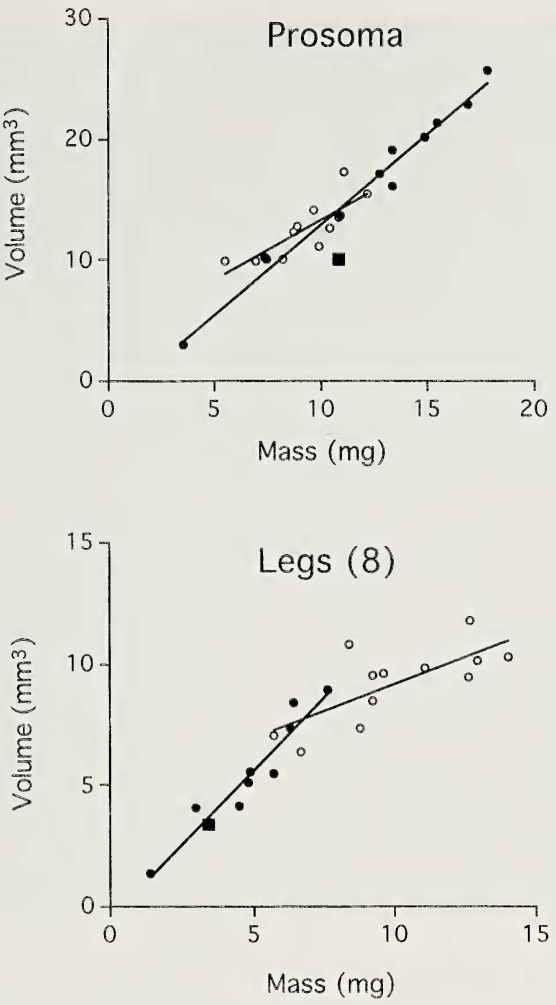


Figure 5.—Relationships between volumes (source: images) and masses (source: balance) for the prosoma and legs of *Scytodes* (filled symbols) and *Schizocosa* (open circles). For the spitting spiders, masses and volumes of both body parts were strongly correlated (prosoma: $r = 0.991$, $P < 0.0001$; legs: $r = 0.960$, $P < 0.0001$). The correlations were also highly significant but less strong for the wolf spiders (prosoma: $r = 0.827$, $P = 0.0009$; legs: $r = 0.730$, $P = 0.007$). Data from the single *Scytodes fusca* specimen (solid square) were included in the two calculations of r for *Scytodes*.

as demonstrated experimentally by Rovner (1978, 1980). The first pair of legs is particularly important for these tasks. The spitting spider, *Scytodes*, enmeshes its prey in a toxic and gummy silk ejected from the spider's fangs, then bites after the prey is immobile. Not surprisingly, these contrasting prey capture techniques are associated with different supporting morphology (Table 1, Figs. 6–11).

Consider the legs. Strength in these appendages is crucial for the wolf spiders whereas sensitivity to position and to the characteristics of what is touched are crucial for the spitting spiders. Strength (resistance to bending) of a tubular structure such as a spider's femur is directly proportional to the fourth power of the radius, inversely proportional to the length and, of course, varies with the properties of the constituent material (Vogel 1988). Thus it is not surprising that *Schizocosa*'s legs are substantially more voluminous than those of *Scytodes*, that their average width (in the direction most crucial for resisting dorso-ventral loading) is 61% greater, and that they are shorter (Table 1). Given that the first pairs of legs are often the ones most used in holding

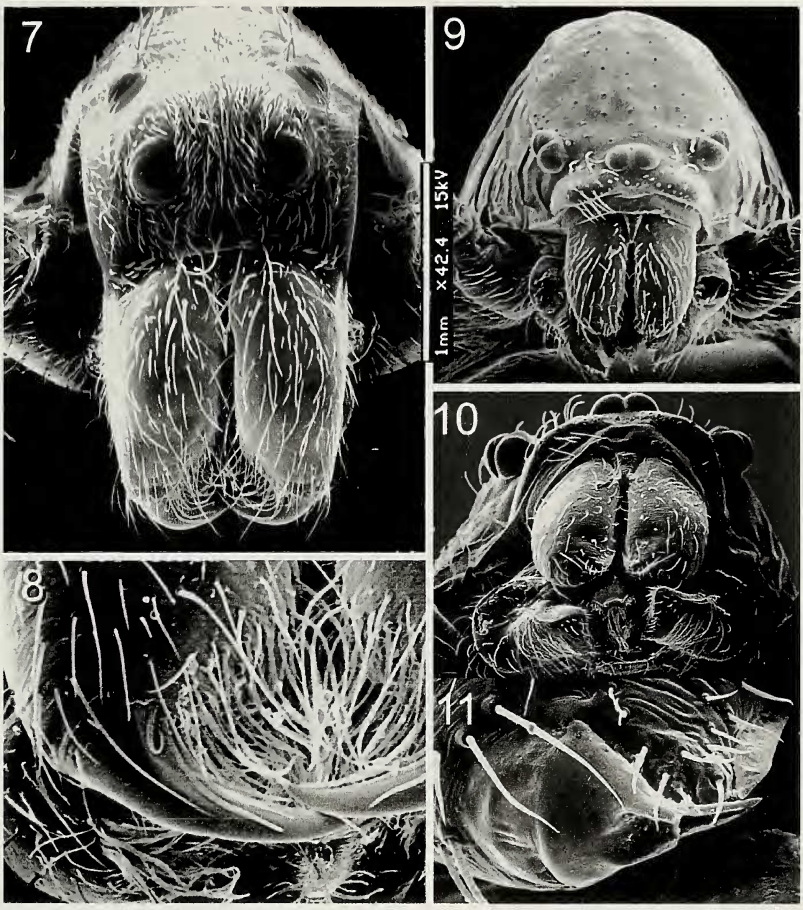
Table 1.—Volumes and linear dimensions of the component parts of the bodies (excluding the opisthosoma) of spitting spiders and wolf spiders. The widths (*) of legs represent mean width, from the dorsal to the ventral surface. The widths (*) of chelicerae represent mean width, from the lateral to the medial surface. We used 2-tailed *t* tests unless we knew from preliminary observation or from the literature to expect a difference in a particular direction.

Component	Measure	*Scytodes* Mean ± S.E.	*Schizocosa* Mean ± S.E.	Comparison *t*	*P*	Type
Prosoma + legs (8)	volume	22.26 ± 2.76 mm^3	21.63 ± 1.02 mm^3	0.228	0.8218	2-tailed
Prosoma	volume	16.88 ± 2.09 mm^3	12.42 ± 0.68 mm^3	2.186	0.0409	2-tailed
Legs (8)	volume	5.37 ± 0.74 mm^3	9.21 ± 0.46 mm^3	4.544	<0.0001	1-tailed
Chelicerae (2)	volume	0.12 ± 0.01 mm^3	0.69 ± 0.06 mm^3	8.035	<0.0001	2-tailed
Venom glands (2)	volume	2.45 ± 0.35 mm^3	0.08 ± 0.01 mm^3	7.483	<0.0001	1-tailed
Prosoma	width	2.78 ± 0.17 mm	2.43 ± 0.06 mm	2.06	0.0527	2-tailed
Chelicera	length	0.59 ± 0.03 mm	1.09 ± 0.02 mm	14.24	<0.0001	1-tailed
Chelicera	width*	0.32 ± 0.01 mm	0.55 ± 0.02 mm	7.972	<0.0001	2-tailed
Fang	length	0.13 ± 0.01 mm	0.63 ± 0.02 mm	22.392	<0.0001	1-tailed
Legs (mean)	length	19.61 ± 1.77 mm	13.80 ± 0.65 mm	3.306	0.0035	2-tailed
Legs (mean)	width*	0.18 ± 0.01 mm	0.29 ± 0.01 mm	9.332	<0.0001	1-tailed
Leg ratio (fore/hind)	length	1.377 ± 0.24	0.752 ± 0.02	22.385	<0.0001	2-tailed
Leg ratio (fore/hind)	width*	0.912 ± 0.01	1.153 ± 0.02	10.680	<0.0001	2-tailed

prey (Rovner 1980), it is likewise not surprising that in *S. duplex* the first legs are 25% more stout than the hind legs. Chemical and tactile sensitivity, on the other hand, does not depend on structural strength, but length does confer a greater radius of discovery for the sensory organs on the legs. Thus, for the predatory technique used by spitting spiders, long legs that need not be robust are suitable. All of this, even the tendency of *Scytodes* to have longer forelegs than hind legs (but not the converse tendency in *Schizocosa*), supports the assertion that leg properties constitute part of an adaptive suite of morphological characters that enhance the effectiveness of predation for both groups of spiders.

Chelicerae, and the fangs they bear, can be considered in the same way, although here the role of morphological size in the spitting spiders is less clear. Given the predatory technique of the wolf spiders, mechanically strong chelicerae equipped with teeth and bearing long fangs clearly contribute to a wolf spider's ability to restrain prey until venom is delivered via the fangs (Rovner 1980). But why are the chelicerae of *Scytodes* small but not delicate (they have about the same ratio of length to breadth, 1.84:1, as those of Schizocosa,

Figure 6.—A pair each of venom glands from *Scytodes* (left) and *Schizocosa* (right) shown to scale. The spitting spider glands are shown in lateral (top) and dorsal (bottom) views. The venom glands of the wolf spider are nearly cylindrical. The mass of opaque material occupying much of the lateral view of the *Scytodes* gland is the glandular contents (Kovoor & Zylberberg 1972).



Figures 7–11.—SEM images of *Schizocosa* (7, 8) and *Scytodes* (9–11). The chelicerae and fangs are conspicuous components of the frontal view of the wolf spider but are relatively smaller in spitting spider—the fangs of *Scytodes* are nearly invisible when the spider is not about to spit (9) and can only clearly be seen when viewed from below (10, 11). The scale bar applies only to Figs. 7 & 9.

1.98:1), and why are the fangs so disproportionately small (Table 1)? Although further study will be required to answer these questions, we offer two hypotheses. First, the width of the spitting spider's chelicera probably serves to accommodate the larger than normal venom duct that must conduct a viscous mixture of silk, glue, and venom at high velocity. And second, that the diminutive fang facilitates its very rapid oscillation and, in turn, makes possible the characteristic zigzag pattern (Gilbert & Rayor 1985; Foelix 1996) of silk deposition. If this second hypothesis were correct, fang length would then be a good example of evolutionary compromise, in this case between selection for shortness (facilitating oscillation through a reduction in angular momentum) and selection for increased length (facilitating chitin penetration and, ultimately, venom delivery to the interior of prey items). The resolution of the compromise at a fang length too short for effective penetration of thick chitin may have abbreviated the menu of acceptable prey types for spitting spiders (Nentwig 1985).

Resource allocation.—*Scytodes* allocates much less of its total resource pool to overtly predatory structures (chelicerae, venom glands) than does *Schizocosa* (chelicerae, venom glands, and legs) (Fig. 12). When we include the legs of *Scytodes* in this comparison, perhaps legitimate both because they serve a sensory role in predation and because they may be lost relatively frequently during predation (Ades & Ramires 2002), the disparity between the two patterns of allocation de-

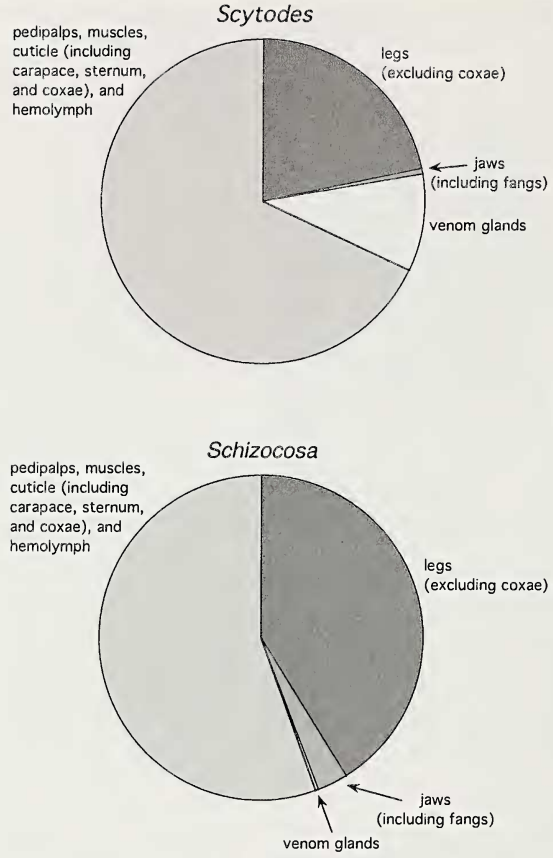


Figure 12.—Mean allocation of resources (as % of non-opisthosoma volume) in spitting spiders (above) and wolf spiders (below). The volume of the grouping of tissues on the left in each chart was estimated by subtraction from the mean volume (excluding the opisthosoma) of the spiders in each species.

creases but remains conspicuous. Moreover, much of the volume of the venom glands of spitting spiders is occupied by secreted products, is not biomass per se, and may be lost to the spider (if recycling does not occur) during predation attempts. Thus spitting spiders employ a predatory technique that appears not to rely on the production and maintenance of large structures.

On the other hand, both spitting and wolf spiders use their legs in locomotion, in mating, and in other activities, so it is not clear that the allocation of resources to legs should be considered as an allocation to predation even when, as in *Schizocosa*, those appendages are entirely necessary for prey capture. If legs are excluded from our consideration, then the fundamental difference between spitting and wolf spiders' allocation patterns is that the former favors the production of venom gland secretions and the latter favors massive chelicerae.

These two views of allocation cannot be reconciled without evaluating them in the context of the phylogeny of the two spider groups, a task that will require further study. For the moment, however, we note the following. First, none of the spider families that are close relatives of the Scytodidae have members that capture prey by spitting, but they do contain members with body plans that resemble those of the spitting spiders (e.g., Pholcidae: Nentwig 1985). And second, many of the spider families that are close relatives of the Lycosidae have members that capture prey by grabbing and biting, and most have body plans that closely resemble that of *Schizocosa*. Further study, then, could reveal that part of the allocation pattern we have described for the spitting spiders is not so much a conse-

quence of their predatory technique as it is a consequence of phylogenetic inertia (Orzack & Sober 2001).

ACKNOWLEDGMENTS

We are particularly indebted to Andrew Douglas for his generous donation of time and the use of his fine microscopy suite. We also thank Patricia R. Miller, Hank Guarisco, James Carrel and Gerald Baker for providing us with some of the spiders used in this study and Jerry Calvin for his help with the scanning electron microscope. The study was supported in part by Vassar College's Class of '42 Faculty Research Fund.

LITERATURE CITED

Ades, C. & E.N. Ramires. 2002. Asymmetry of leg use during prey handling in the spider *Scytodes globula* (Scytodidae). Journal of Insect Behavior 15:563–570.

Bristowe, W.S. 1931. Notes on the biology of spiders, IV. Annals & Magazine of Natural History 8:469–471.

Calder, W.A. 1984. Size, Function, and Life History. Harvard University Press, Cambridge, 431 pp.

Dabelow, S. 1958. Zur Biologie der Leimschleuderspinne *Scytodes thoracica* (Latreille). Zoologische Jahrbucher, Abteilung fur Systematik, Okologie und Geographie der Tiere 86:85–126.

Foelix, R.F. 1996. Biology of Spiders (2nd ed.). Oxford University Press, Oxford. 330 pp.

Gilbert, C. & L.S. Rayor. 1985. Predatory behavior of spitting spiders (Araneae: Scytodidae) and the evolution of prey wrapping. Journal of Arachnology 13:231–241.

Huxley, J.S. 1932. Problems of relative growth. Dial Press, New York, 276 pp.

Jackson, R.R. & S. D. Pollard. 2001. How to stalk a spitting spider. Natural History 110:16–18.

Kovoor, J. 1987. Comparative structure and histochemistry of silk-producing organs in arachnids. Pp. 160–186. *In* Ecophysiology of Spiders. (W. Nentwig. ed.) Springer-Verlag, New York, 448 pp.

Kovoor, J. & L. Zylberberg. 1972. Histologie et infrastructure de la glande chélicérienne de *Scytodes delicutula* Sim. (Araneidae, Scytodidae). Annales des Sciences Naturelles, Zoologie, Paris 14:333–388.

MacAlister, W.H. 1960. The spitting habit of the spider *Scytodes intricata* Banks (Scytodidae). Texas Journal of Science 12:17–20.

Millot, J. 1929. Sur la glande céphalothoracique d'une Araignée (*Scytodes thoracica* Latr.). Comptes Rendus de L'Academie des Sciences 119:189.

Millot, J. 1930. Glandes vénimeuses et glandes séricigenes chez les Sicariides. Bulletin de la Societe Zoologique de France 55:150–175.

Monterosso, B. 1928. Note arachnologiche.—Sulla biologia degli Scitodidi e la ghiandola glutinifera di essi. Archivio Zoologico Italiano 12:63–122.

Nentwig, W. 1985. Feeding ecology of the tropical spitting spider *Scytodes longipes* (Araneae,Scytodidae). Oecologia 65:284–288.

Opell, B.D. 1997. A comparison of capture thread and architectural features of Deinopoid and Araneoid orb-webs. Journal of Arachnology 25: 295–306.

Orzack, S.H. & E. Sober. 2001. Adaptationism and optimality. Cambridge University Press, New York, 416 pp.

Peters, J.M. 1987. Fine structure and function of capture threads. Pp. 187–202. *In* Ecophysiology of Spiders. (W. Nentwig. ed.) Springer-Verlag, New York, 448 pp.

Rovner, J.S. 1978. Adhesive hairs in spiders: behavioral functions and hydraulically mediated movement. Symposium Zoological Society of London 42:99–108.

Rovner, J.S. 1980. Morphological and ethological adaptations for prey capture in wolf spiders (Araneae, Lycosidae). Journal of Arachnology 8: 201–215.

Vogel, S. 1988. Life's devices: the physical world of animals and plants. Princeton University Press, Princeton, 367 pp.

Walker, S.E. & A.L. Rypstra. 2001. Sexual dimorphism in functional response and trophic morphology in *Rabidosa rabida* (Araneae: Lycosidae). American Midland Naturalist 146:161–170.

Walker, S.E. & A.L. Rypstra. 2002. Sexual dimorphism in trophic morphology and feeding behavior of wolf spiders (Araneae: Lycosidae) as a result of differences in reproductive roles. Canadian Journal of Zoology 80:679–688.

Manuscript received 14 April 2003, revised 18 February 2004.